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Book review: The Natural History of Burnet Moths, Part I

Gerhard M. Tarmann[1]

1 *Naturwissenschaftliche Sammlungen, Sammlungs- und Forschungszentrum der Tiroler Landesmuseen, Krajnc-Straße 1, A-6060 Hall, Austria; g.tarmann@tiroler-landesmuseen.at*

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Preamble. Exactly three weeks have passed since I spotted the parcel with "The Book" in the foyer behind the entrance door. I had just returned from a five-week field trip to Liguria and Catalonia and was in the best mood. In this emotional moment, after having opened the parcel and seen it for the first time, I thought: 'Praised be this day! Here it really is! "The Book"!'. These hardcover bound 630 pages with their 3.2 kg weight meant a lot to me. They are not only the first part (of three) of another book on burnet moths, they are a piece of the souls of two of my best friends and colleagues both of whom dedicated their lives to the study of Zygaenidae, like myself, and have put all their knowledge and that of many colleagues, friends and supporters together in an impressive monograph on the life history of the Zygaeninae, the burnet moths, the best known subfamily of this almost mystic group of Lepidoptera.

I had been asked to write a book review for Nota Lepidopterologica earlier and started to read almost immediately. A day later I was not only full of excitement, I was also irritated and emotionally at rock bottom. Too many personal remembrances had mixed with admiration and respect for how such a work could ever have been written. Only one year ago I had been on a wonderful field trip together with W. G. 'Gerry' Tremewan in Italy. We lost Gerry on 1 October 2016 just after Axel Hofmann had managed to show him the first chapters of their book ready for print. That he will never be able to see the now published printed version is really tragic. However, at least he had had the satisfaction to know this work was in the skillful hands of Axel and the knowing English editorship of Adrian Spalding, another old friend. During this last field trip to Italy in 2016 Gerry had talked about this book much more than he had on all earlier trips during the 20 years that we had had together. Every time he spoke about this work he was so full of vivacity and joy that even my own field work seemed almost irrelevant. It was always the search in the field for the authentic observation that can only be found by continous personal experiences, exact documentation and meticulous comparison of facts that Gerry emphasised. He saw taxonomy more as a necessary burden that has also to be dealt with but his heart beat for the life history, genetics, distributional patterns and ecological phenomena. Gerry had found a congenial joint author in Axel Hofmann, who compiled an enormous amount of information from his and friends' own experiences and combined it with all Gerry's knowledge to create the manuscript, illustrated it with thousands of figures and pictures and finally skilfully edited and laid out the whole book.

It has taken me three weeks to recover from my feelings but this morning (it is the 26 July 2017), when an icy north-east wind of a rainy summer day in the Alps shook my window and the snow could be seen on the mountain tops when the clouds allowed sight for a short moment, I felt new power and the necessary strength of mind came back to allow me to write about a work that can only be commented on when in such good spirit and mood. It was this spirit of enthusiastic lepidopterists that was the beginning and will be the end of

this remarkable book project on burnet moths and which will hopefully enlighten those who are ready and sensitive enough to read themselves deeper into "The Book" that is, without any doubt, a milestone in entomological literature. For me it is not only a personal honour to be allowed to comment on it but also a great challenge. Knowing that I can hardly do justice to this outstanding work and can only do my best considering the shortcomings of a reader who has never dealt with burnets in such depth and is mainly working on other subfamilies of Zygaenidae, I hope to be able to find the right words to inspire readers to enjoy "The Book" (Fig. 1) with all its unique authentic information and beautiful pictures.

Axel F. Hofmann and W. Gerald Tremewan (2017): The Natural History of Burnet Moths (*Zygaena* Fabricius, 1775) (Lepidoptera: Zygaenidae). Part 1. Proceedings of the Museum Witt Munich 6 (1). Munich and Vilnius. 631 pp., 4663 figures (distribution maps, colour figures, black and white genitalia figures), 73 tables. Hardback. ISBN 978-3-940732-32-3. Price: 150 €*.

This book is the first part of three on the natural history of Zygaeninae (Burnet moths). The world's two most renowned specialists on this group W. Gerald Tremewan (Great Britain) and Axel F. Hofmann (Germany) have combined the results of their life-long studies and produced a breathtaking opus that will without doubt significantly influence all further work on Zygaenidae. The book is dedicated to the two sons of the authors as a symbol to the fact that without the huge support of their families neither the compilation of all the information that is summarised in this book nor the years of production would have been possible.

As acknowledged in the first foreword by Roger L. H. Dennis, the authors, both travellers, explorers and scientists, have achieved an exceptional result in summarizing their dedicated life's work. This book is a culmination of many papers and many journeys, with unselfish scientific comradeship, integrity and respect for the natural world.

The author of the second foreword, Günther Ebert, himself an experienced author, explorer, traveller and field worker, is impressed by the easy way such immense projects can come to fruition if the right persons come together. After an especially enjoyable collecting day in Morocco in the vicinity of Djebel Ayachi in 1989, both authors were sitting over a good cool bottle of rosé wine at their campsite near Midelt in the High Atlas when the idea to write a book on the natural history on burnet moths was agreed upon between them.

The book starts with a preamble that gives the reader a good impression of the long journey from the first idea to the final result. Ups and downs, joy and difficulties in the field, dangerous expeditions, meetings with exceptional friends and supporters, always with the final goal in their minds, the authors claim that they only could manage to finish the book within about a quarter of a century due to modern computer- and phototechnology. What an understatement! Alone the incredible expeditions of Axel Hofmann to Afghanistan in the last years to clear a few still unknown biologies of rare burnets give us an impression with what dedication the authors followed their agreed goal. The preamble ends with the hope that the reader will have as much pleasure with this book as the years of fieldwork, research and compilation of the typescript gave to the authors.

* For orders: hofmann@abl-freibug.de

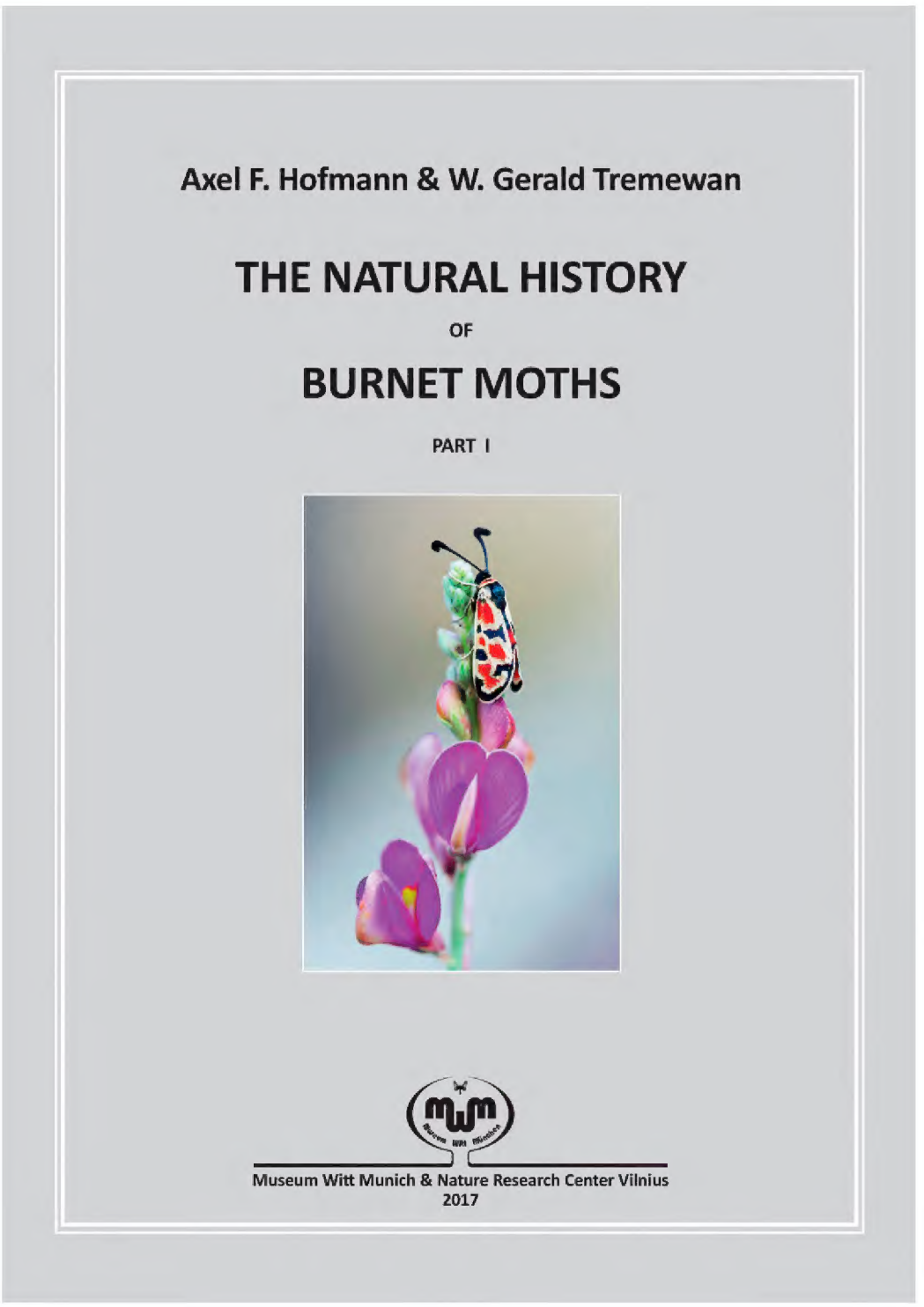
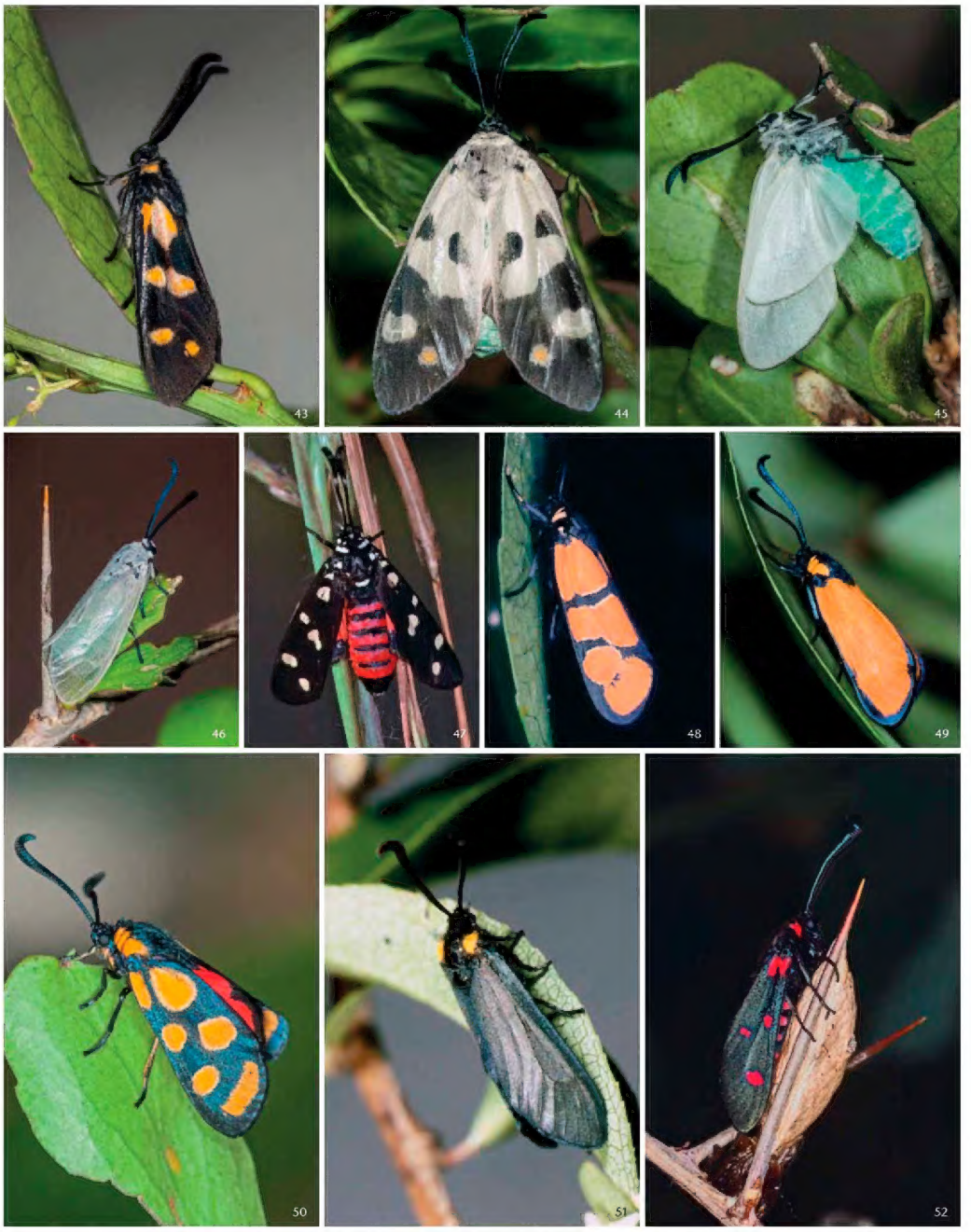


Figure 1. Cover of the book.

Two and a half pages of acknowledgements show how much knowledge is combined in this book. Many of the supporters have passed away in the meantime but their contributions will remain and most of them would be proud to see that they are present in this book.

Each chapter starts with a beautiful double page colour plate.

In the first chapter an overview, with abstracts on the content of all three parts of the whole work, is given after a short introduction. In 22 chapters (1–8 in part I and 9–22 in part II) information on all relevant contents such as the origin, phylogeny, systematics, distribution, zoogeography, morphology, variation, life history, phenology, reproductive biology, genetics, biochemical specialties, aposematism, mimicry, predators, parasitoids, and conservation of burnets is given. Part 3 of the book deals with the burnet species one by one in detail. Here all the field and rearing observations of the authors including the information that they received from others are summarised with special emphasis on their geographic differences.



Figs 43–52. Phenotypic diversity and evolutionary development of Zygaeninae moths (II). 43, *Orna contraria*, ♂ (South Africa: Eastern Cape, Hoegsback SW., e.l. 23.ii.2015). 44, *O. contraria*, ♀ (same locality, 15.ix.2015). 45, 46, *O. nebulosa*, ♀ (same locality, e.l., 8.iii.2014). 47, *Zutulba namaqua zelleri* (South Africa: Limpopo, Pietersburg, 9.i.1985). 48, *Praezygaena myodes* (South Africa: Hogsback, 12.ii.1986 (*N. Duke*)). 49, *P. ochroptera* (South Africa: Haenertsburg, 10 km W., 3.iii.2000, e.l.). 50, *P. agria* (South Africa: Pietersburg, 21 km S., e.l. 19.iii.2014). 51, *Epiorna abessynica* (Ethiopia: Goha Tsiyon, x.1989). 52, *Reissita simonyi* (Oman, Dhofar, e.l. 27.iv.2000). *Photos*: A. Hofmann (43–46, 50), C. M. Naumann (47–49, 51, 52).

Figure 2. Phenotypic diversity in burnet moths on page 18 of the book.

Chapter two deals with the origin, phylogeny, outgroups and systematics of the subfamily Zygaeninae starting with a close up photo of the first fossil zygaenid specimen that has been published, *Zygaena miocaenica* Reiss, 1936. All well preserved fossil Zygaeninae are figured. Phylogenetic relationships are discussed and graphically explained and the distributions of all Zygaeninae genera are shown in colour maps. This is followed by a beautiful double page colour plate of water colour paintings by Crapon de Caprona (1984) in which most of the currently known non-Palaearctic Zygaeninae species are figured. Biotope photos and excellent photos of living specimens by Axel Hofmann and Clas M. Naumann show the phenotypic diversity of adults and larvae (Figs 2–3). Moreover, the types of oviposition, the diversity of habits of the early stages, and the diversity of the cocoons including their ultrastructure are figured and discussed. After this overview the genus *Zygaena* Fabricius, 1775, is treated in detail. The authors' opinion on the phylogenetic relationships based on the published tree of Niehuis *et al*. (2007) is explained and comments on subgeneric and

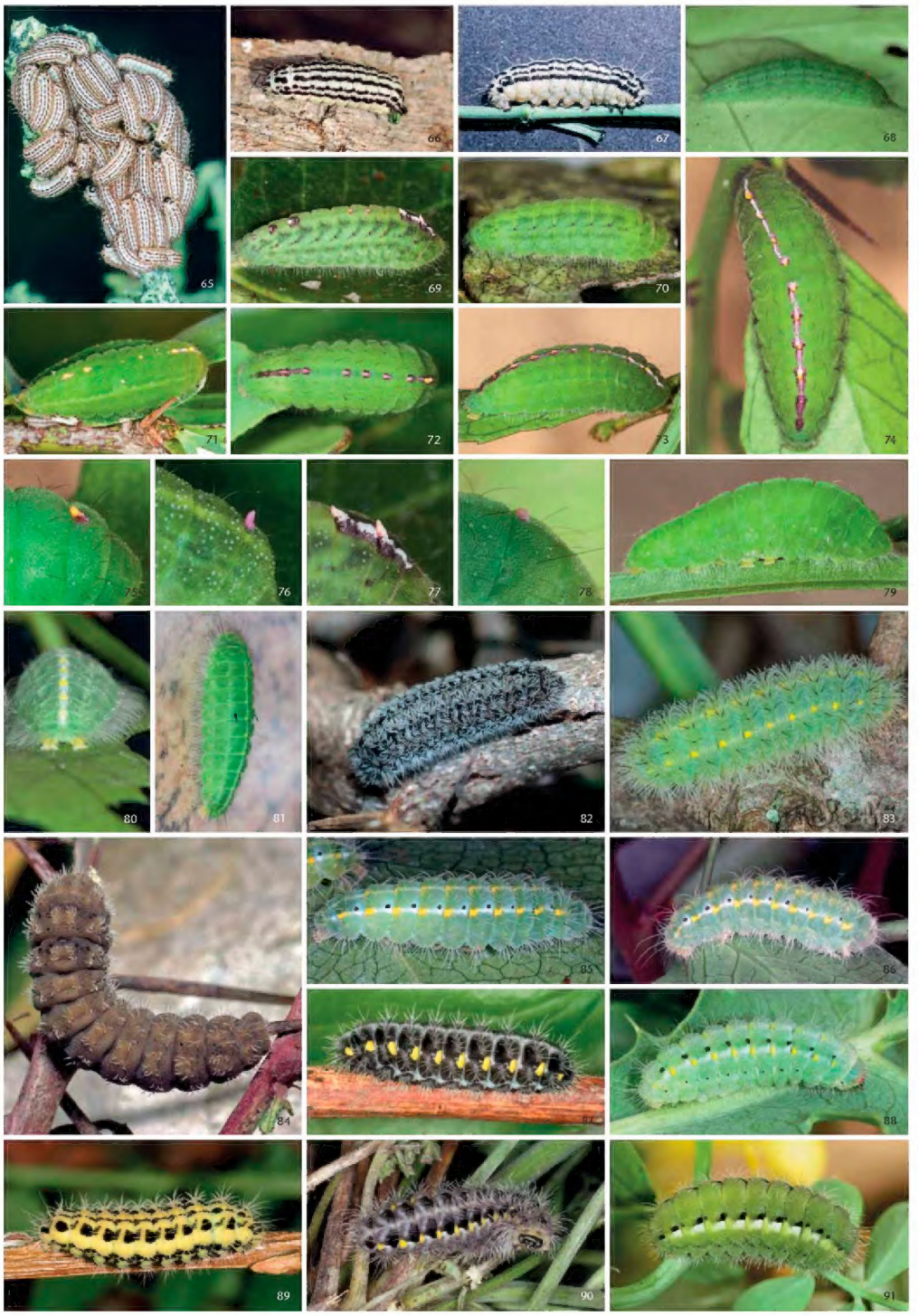


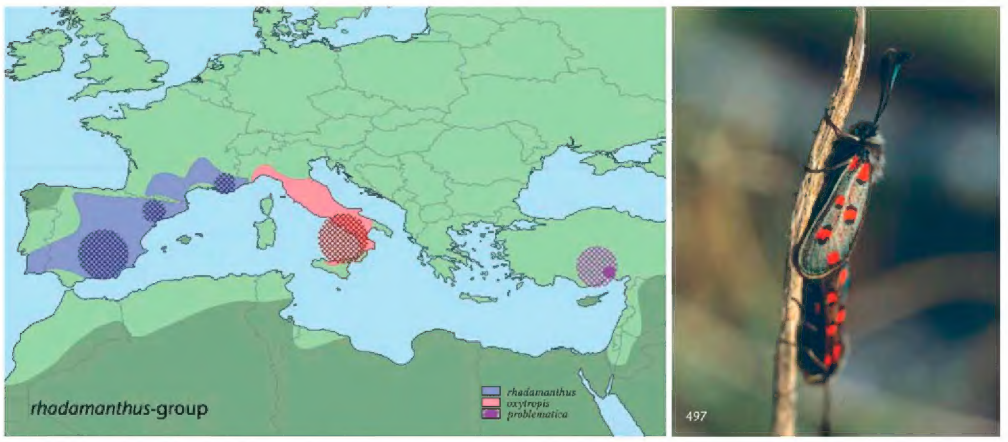
Figure 3. Larval diversity in burnet moths on page 20 of the book.

infrasubgeneric taxonomy are given. The three accepted subgenera *Mesembrynus*, *Agrumenia* and *Zygaena* are further commented on in detail and the possible origin, differentiation and current centres of diversity of the genus *Zygaena* are discussed in depth. Arguments about the possible centre of evolution of the genus are presented and compared, all of it illustrated with informative maps and trees. This is followed by a phylogeographic analysis of stem groups, species groups and species.

A complete checklist of the genus *Zygaena* Fabricius, 1775, lists 108 currently accepted species but it is also discussed that some species hybridise and their taxonomic position is still not completely clear.

Chapter three deals with one of the most difficult and unclear species groups, the *Zygaena purpuralis/minos* complex. This chapter impressively shows the challenge that taxonomists have to face when characters are not sufficiently known and, even when the morphology, biology and distribution is known, how difficult it is to decide as a scientist how to draw the right conclusions

136 *Distribution and zoogeography*



Figs 496, 497. Refugia and current distribution of the *rhadamanthus*-group. 496, map showing ranges of *Zygaena rhadamanthus*, *Z. oxytropis* and *Z. problematica* (range of genus *Zygaena* in light green). 497, *Z. rhadamanthus guichardi*, the westernmost population with strongly isolated spots 5 and 6 (Portugal: Carrapateira vic., 50–100 m, 19.iii.1989). *Photo*: W. G. Tremewan.

Figs 498–500. Diversification of the *rhadamanthus*-group, from west to east. 498, *Zygaena rhadamanthus rhadamanthus* (France: Roussillon, 20.v.2013). 499, *Z. oxytropis oxytropis* (Italy: Potenza, Monte Sirino N., Tepe di Roccarossa S., 1,360–1,400 m, e.l., 8.v.2011, S). 500, *Z. problematica* (Turkey: Çamlıyayla 10 km E., 28.v.1995). Note the change in the black edging of the spots and in the distances between spots 5+6, which are widely separated in the westernmost populations in Portugal, closer in southern France, and connected in populations in the Apennines (*Z. oxytropis*) and in southern Turkey (*Z. problematica*). *Photos*: J.-M. André (498), A. Hofmann (499), C. M. Naumann (500).

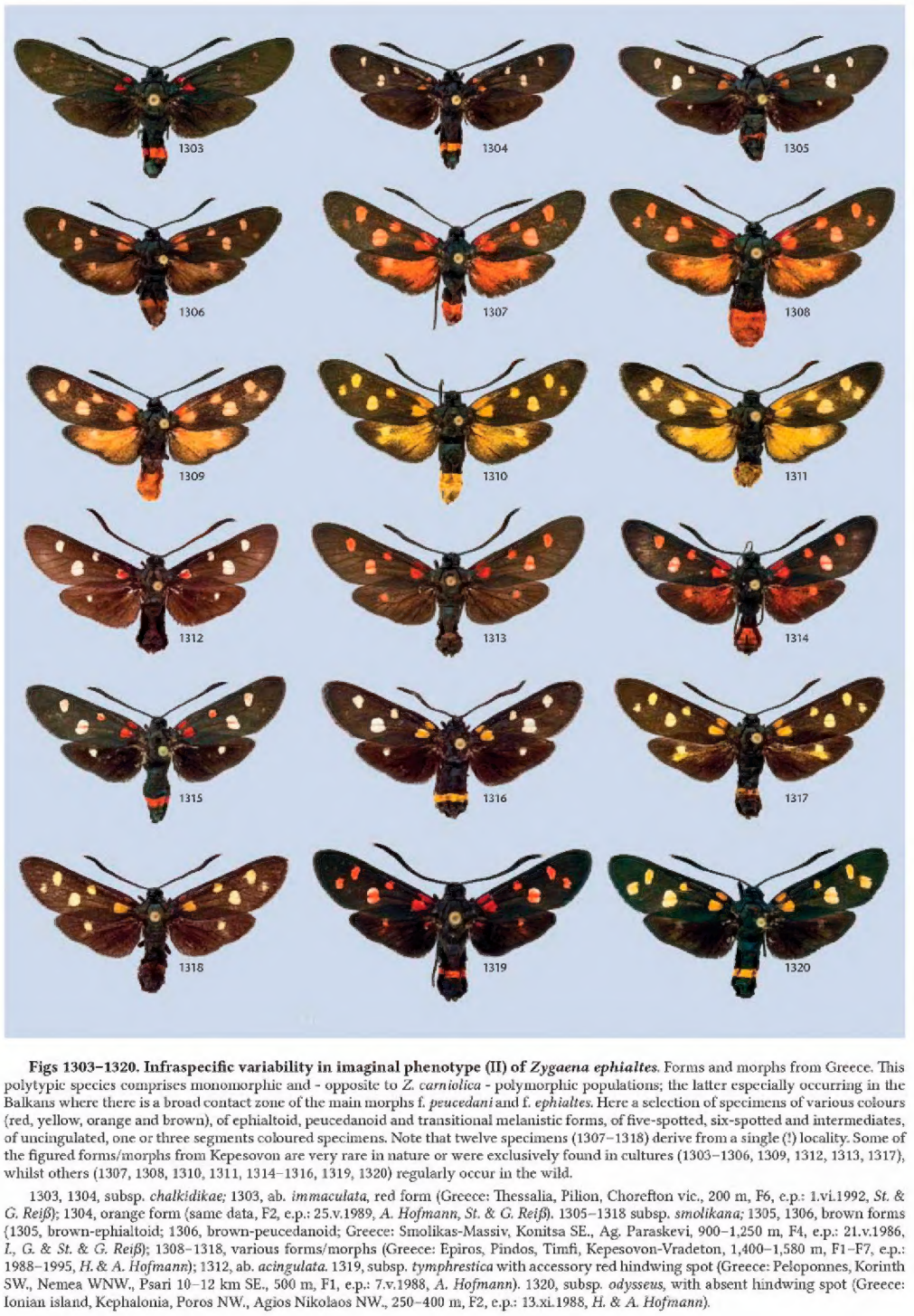
The *rhadamanthus*-group. *Zygaena rhadamanthus*, *Z. oxytropis* and *Z. problematica*, comprising the *rhadamanthus*-group, represent a very good example of three allopatric species that are associated with a clearly defined phenotypic character progression, suggesting that the group expanded from west to east and not from east to west, as Naumann (1966: 17) and Naumann, Tarmann & Tremewan (1999: 50, text-fig. 51) interpreted. It is here suggested that the correct interpretation of the geographical character progression expressed in the *Z. rhadamanthus*-group is *Z. rhadamanthus* → *Z. oxytropis* → *Z. problematica*. For example, with reference to the phenotypes of these three species, many populations of *Z. rhadamanthus* have a pronounced, red abdominal cingulum and the forewing spots (except spot 6) are always distinctly edged with black proximally and distally, whereas the cingulum is lacking in *Z. oxytropis* and *Z. problematica* and the black edging of the spots is reduced in the former species and absent in the latter, i.e. in phylogenetic terms, characters are lost instead of acquired. Moreover, it is easier to understand (and more parsimonious) if one deduces the derivation of the character-reduced species *Z. oxytropis* and *Z. problematica* from *Z. rhadamanthus*, i.e. the loss of cingulum, instead of postulating the development of this feature from non-cingulated forms. Less plausible also would be the

Figure 4. An example of the distribution and zoogeography of burnet moths on page 136 of the book.

from the summarised facts. All arguments are nicely accompanied by good illustrations of specimens, larvae and genitalia of males and females.

Chapter four is a real highlight of the book. It is dedicated to zoogeography, the distributional patterns of the various species, the diversity of habitats, possible historical origins of populations, refugia and distributional pathways, endemism, expansion and invasion of areas and habitats and phylogeography, and concludes with a profound and impressive comparative analysis of the 15 presented and discussed geographic subareas where *Zygaena* currently lives (Fig. 4). Alone this chapter could form an impressive book of its own. On 190 pages, illustrated with hundreds of excellent pictures of specimens, habitats, distribution maps, tables, graphics and trees the authors present a firework of informational highlights showing their great enthusiasm and outstanding knowledge.

Chapter five deals with the morphology of the adults and the early stages of *Zygaena*. The figures in this part of the book are partly taken from the late Clas M. Naumann's huge archive



Infraspecific variability in Zygaena ephialtes 341

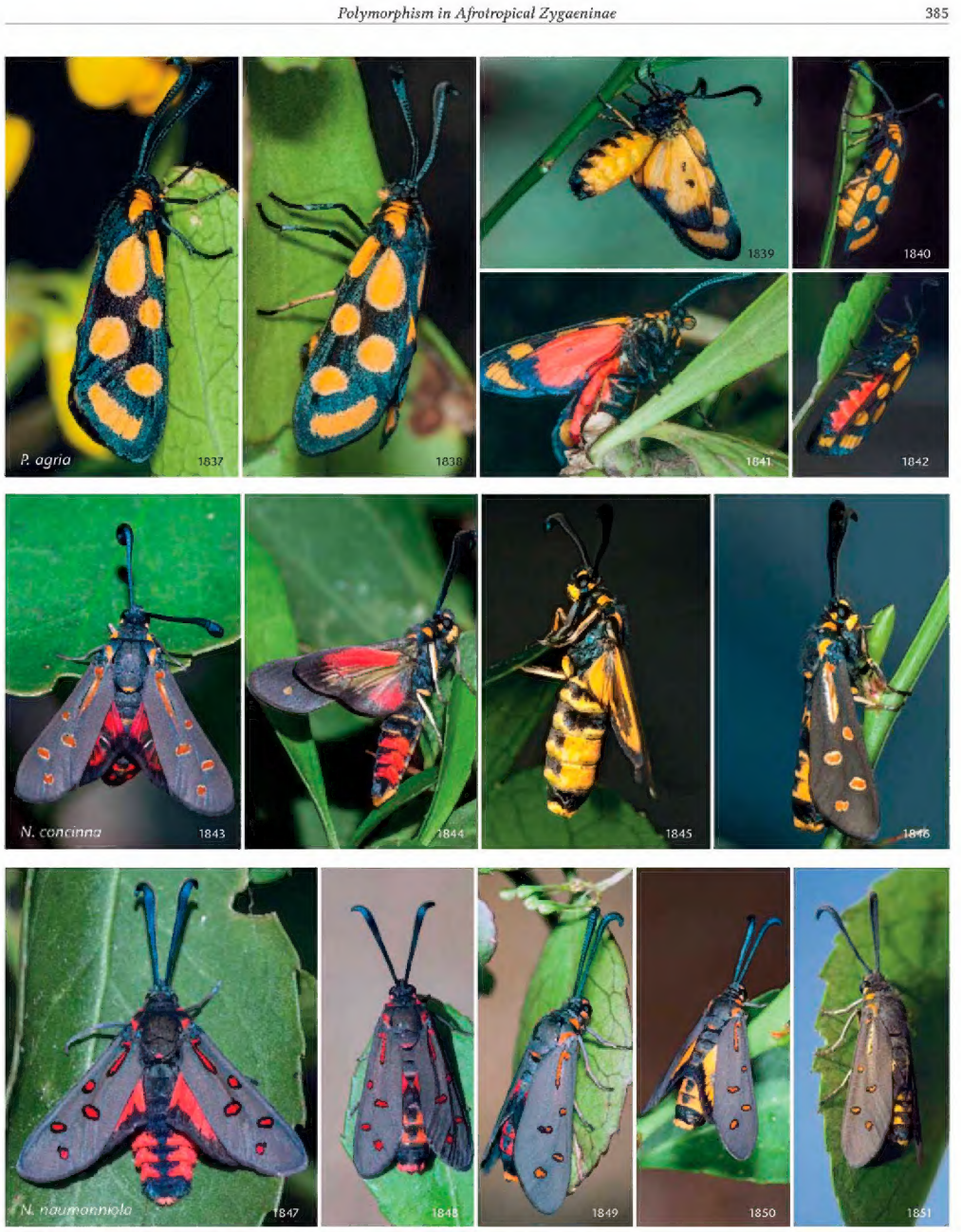
Figs 1303–1320. Infraspecific variability in imaginal phenotype (II) of *Zygaena ephialtes*. Forms and morphs from Greece. This polytypic species comprises monomorphic and - opposite to *Z. carniolica* - polymorphic populations; the latter especially occurring in the Balkans where there is a broad contact zone of the main morphs f. *peucedani* and f. *ephialtes*. Here a selection of specimens of various colours (red, yellow, orange and brown), of ephialtoid, peucedanoid and transitional melanistic forms, of five-spotted, six-spotted and intermediates, of uncingulated, one or three segments coloured specimens. Note that twelve specimens (1307–1318) derive from a single (!) locality. Some of the figured forms/morphs from Kepesovon are very rare in nature or were exclusively found in cultures (1303–1306, 1309, 1312, 1313, 1317), whilst others (1307, 1308, 1310, 1311, 1314–1316, 1319, 1320) regularly occur in the wild.

1303, 1304, subsp. *chalkidikae;* 1303, ab. *immaculata*, red form (Greece: Thessalia, Pilion, Chorefton vic., 200 m, F6, e.p.: 1.vi.1992, *St. & G. Reiß*); 1304, orange form (same data, F2, e.p.: 25.v.1989, *A. Hofmann, St. & G. Reiß*). 1305–1318 subsp. *smolikana;* 1305, 1306, brown forms (1305, brown-ephialtoid; 1306, brown-peucedanoid; Greece: Smolikas-Massiv, Konitsa SE., Ag. Paraskevi, 900–1,250 m, F4, e.p.: 21.v.1986, *L, G. & St. & G. Reiß*); 1308–1318, various forms/morphs (Greece: Epiros, Pindos, Timfi, Kepesovon-Vradeton, 1,400–1,580 m, F1–F7, e.p.: 1988–1995, *H. & A. Hofmann*); 1312, ab. *acingulata*. 1319, subsp. *tymphrestica* with accessory red hindwing spot (Greece: Peloponnes, Korinth SW., Nemea WNW., Psari 10–12 km SE., 500 m, F1, e.p.: 7.v.1988, *A. Hofmann*). 1320, subsp. *odysseus*, with absent hindwing spot (Greece: Ionian island, Kephalonia, Poros NW., Agios Nikolaos NW., 250–400 m, F2, e.p.: 13.xi.1988, *H. & A. Hofmann*).

Figure 5. Infraspecific variability in burnet moths on page 341 of the book.

that has been provided to Axel Hofmann by Storai Naumann for publication in this book. Clas Naumann did a lot of innovative work on zygaenids in his time as professor of zoology in the university of Bielefeld in the early 1980s including the first series of stereoscan pictures. Many of these results were still unpublished at his death and are presented here for the first time. Throughout their lives both Axel Hofmann and Gerry Tremewan were not just gifted field workers but also keen breeders of *Zygaena* and this has led to an archive of photos of eggs, larvae, pupae, cocoons and adults that has no comparison worldwide. Thousands of pages of notes about the habits of all stages are stored in this archive. Only a small part of these treasures could be presented in this book but even that is more than enough to illustrate the peculiarities in structure and life of *Zygaena*.

Chapter six deals with the well known variability in the phenotype of adults and larvae of *Zygaena*. On 59 pages and illustrated with 652 colour figures this chapter gives the reader an idea



Figs 1837–1851. Polymorphism in Zygaeninae (II). Afrotropical taxa (I). Sex-independent polymorphism of yellow and red forms from South Africa. 1837–1842, *Praezygaena agria*. This dimorphism is hardly visible when the wings are closed as it is only expressed on the hindwings and the abdomen, while the tegulae, collare and other characters remain uniform (Limpopo, Pietersburg ca. 30 km N., 1,350 m, e.l., e.p.: 19.iii.–18.vi.2014, S). 1843–1846, *Neurosymploca concinna*. Here the dimorphism is recognizable with closed or open wings. While the tegulae and collare are only weakly changed in colouration, the change from red to yellow is complete on the wings (1843, 1844, Western Cape, Oudtshoorn NW., Gr. Swartberg pass, 1,000 m, 1.iii.2016, S; 1845, 1846, Eastern Cape, Hoegsback SW., 850 m, e.o., 18.vi.2014, S). 1847–1851, five distinct colour morphs of *N. naumanniola*; 1847, pure red form (Western Cape, Leipoldtville N., 120 m, e.l., 12.iii.2016); 1848, red wings, orange abdominal cingulum (Western Cape, Lambertsbaai 16 km ESE., 100 m, e.l., 1.iii.2016); 1849, 1850 (Western Cape, Nieuwoudtville W., Van Rhyns pass, 730 m); 1849, (orange forewings and tegulae, red hindwings and cingulum; e.l., 26.ii.2015); 1850, (orange forewings and tegulae, yellow hindwings and cingulum; e.o., 23.v.2016); 1851, complete yellow form (Western Cape, Piketberg W., Versfeld pass, 570 m, e.l., 24.ii.2016). *Photos*: A. Hofmann.

Figure 6. An example of the polymorphism in burnet moths on page 385 of the book.

why *Zygaena* has been one of the most popular genera for collectors and photographers and a model group for studies about variation. Axel Hofmann's exceptional selection of specimens for this chapter enables easy understanding of complicated phenomena and shows much skill by the authors in educating the reader to look and understand (Fig. 5). Many non-Palaearctic Zygaenini are also figured showing the same polymorphism as many species of *Zygaena* (Fig. 6).

Chapter seven is dedicated to geographical patterns and clusters in *Zygaena*. It deals with the interesting question of supraspecific phenomena and characters bound to special geographical regions, called by the authors 'pheno-geography'. An important example is the syntopic occurrence of melanistic subspecies of different *Zygaena* species in several regions of their distribution, both larvae and adults. But there are more such phenomena known, such as an increase of red or white

coloration in certain regions. Again the information is perfectly summarized by the authors, richly illustrated and accompanied by informative distribution maps.

Chapter eight gives an overview on historical observations and publications on the biology of burnet moths, starting with a frontispiece that shows *Zygaena* species in a ca. 260-year-old oil painting by Otto Marseus van Schrieck housed in the Simferopol Art Museum in Crimea and discussed by Efetov & Tarmann in 2007 [Efetov KA,Tarmann GM (2007) Van Schrieck's burnet moth – an image of a *Zygaena* species (Lepidoptera: Zygaenidae) a century before Linnaeus. Entomologist's Gazette 59: 62–64, figs 1–2]. However, the reader learns that the oldest known illustration of a *Zygaena* is figured in Cocharelli's medieval work *Leaves from a prose treatise on the Seven Vices* dated from between 1330 and 1340 which clearly shows a Mediterranean *Zygaena lavandulae*. The authors then give a summary starting from pre-Linnaean observations up to today mentioning all important authors who have dealt, in some way, with the natural history of *Zygaena*. They illustrate this chapter with original portraits and many reproductions of colour plates. The fact that Gerry Tremewan was, for many years, the professional editor-in-chief of the British Museum's Bulletin (Natural History) and in retirement maintained good connections to the world's best library of old books on natural history was clearly a unique advantage and the deep respect and love of the authors for history and literature can be felt on each page. The chapter ends with an illustrated report on the 14 international symposia on Zygaenidae held between 1980 and 2014 with a summary of their content.

These eight chapters are followed by a short introduction on the genital morphology of *Zygaena* and black and white photos of the relevant diagnostic characters of the male and female genitalia of all known species.

The references, a glossary of special terms and an alphabetic index finish this amazing book.

Conclusion

Hofmann & Tremewan's 'The Natural History of Burnet Moths' is a never before seen monumental opus on the subfamily Zygaeninae of Zygaenidae in all its diversity and beauty. Already the now published first part gives the impression of the complete final work as a milestone in entomological history. It is of unique completeness, illustrated with thousands of excellent pictures, graphics and maps. It is the result of the collaboration of two enthusiastic authors summarising their lifelong studies of literature, collections, observations in nature, rearing experiments, and endless discussions between the authors and other scientists. The spirit of joy for this work can be felt on each page and it is immensely inspiring to go through the chapters step by step learning a lot and being surprised by the sheer unbelievable diversity of life.

Thanks to the financial support of the Thomas-Witt-Stiftung in Munich, the price for this monumental work could be kept on an affordable basis not only for entomologists but also for lovers of beautiful nature books. It only can be heartily recommended to make a present to oneself or friends with this book as a never ending well of joy for the beauty and astonishing diversity of nature.

It is expected from a reviewer to also find some criticism on the work that he is reviewing. But to criticise the few typing errors and missed references that can be recognised in this book seems simply unnecessary.